THE RELATION OF HAIRY AND CUTINIZED COVERINGS TO TRANSPIRATION

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(WITH ONE FIGURE)

Numerous experiments have shown that cutin is a very efficient means of retarding the loss of water from plant tissue. We may cite only such cases as the paring of the apple and its consequent much increased loss of water as shown by weighing, and of various other plant tissues similarly treated. In regard to the function of hairy coverings, however, the lack of experimentation has left us very much in doubt. We find two theories advanced: one holding that such coverings are to retard transpiration, the other that they are to protect the tissue from too intense light. Some have held also that they may, and probably do, serve both purposes, either at the same time or in different cases.

It has long been recognized that hairy coverings must be divided into two classes when function is considered, namely the living and the non-living.[1] The cells of the former contain protoplasm, and therefore are themselves in danger of drying out. Such hairs naturally cannot be used by the plant for restricting loss of water. The non-living hairs, however, are soon free of protoplasmic contents and are filled with air. In such a form, spread out over the plant surface, they may well be conceived of as constituting a restricting screen to the passage of water vapor. By the refraction of light from the contained air this type of hair may also act as a light screen. We shall have to do, therefore, only with this latter group in the following pages.

Experimental evidence for or against either of these theories of the function of air-containing plant hairs is very meager, however, and this is the more remarkable when the very common occurrence

[1] FLEISCHER, E., Die Schutzeinrichtungen der Pflanzenblätter gegen Vertrocknung. 16. Bericht. über das K. Realgymnas. zu Döbeln. 1885.

VOLKENS, G., Die Flora der ägyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen. Berlin. 1887.

of such coverings is considered. In the absence of such evidence the following questions have frequently occurred to the writer: 1. Do such coverings actually retard the loss of water sufficiently to justify their maintenance on this basis through natural selection? 2. Is it not highly improbable that coverings so thin as are "strigose" coverings should affect the loss of water in any way, and does not this count as an objection to the water-retarding theory? 3. If the function of hairs is to retard the loss of water, why should some plants employ thick cutin and others a resinous coating instead of plant hairs to attain the same end? 4. Has the relation to light or the relation to loss of water been the principal factor in the evolution of hairy coverings? Since the answering of these questions has seemed to be of rather fundamental importance in the teaching of ecology, an attempt has been made to obtain evidence, either circumstantial or direct, and the results obtained form the basis of this paper.

The few actual experiments with hairy coverings, so far as I have been able to find, may be summarized as follows. KERNER[2] bound two raspberry leaves around two thermometer bulbs in such a way that in one case the green upper leaf surface and in the other case the white tomentose under surface was outermost. When placed in the sun, the mercury in the green bulb rose to a point 2–5° above that in the white bulb. Two more raspberry leaves were entirely removed from the plant and laid side by side in the sun. The one with the green surface uppermost dried and shriveled much sooner than the one with the white surface uppermost. GOEBELER[3] investigated the effect of trichome structures on the stems of ferns. He found by weighing that the living trichomes markedly increased the transpiration. VESQUE[4] found by means of cultural experiments with certain plants that when the dryness increased, the hairy covering increased in density also. BRENNER[5] found that the hairy

[2] KERNER, A., AND OLIVER, F. W., The natural history of plants **1**:314.

[3] GOEBELER, E., Die Schutzvorrichtungen am Stammscheitel der Farne. Flora **69**:487. 1886.

[4] VESQUE, M. J., ET VIET, M. C., De l'influence du milieu sur la structure anatomique des végétaux. Ann. Sci. Nat. Bot. VI. **12**:176. 1881.

[5] BRENNER, M., see BURGERSTEIN, Die Transpiration der Pflanzen 210. 1904.

covering of certain species of Quercus became thicker when exposed to greater intensity of sunlight.

HABERLANDT[6] selected two nearly equal leaves of the same opposite pair from a plant of *Stachys lanata*. The under side of each was coated with cocoa butter, and from the upper side of one the hair was carefully removed with curved scissors. The two petioles were placed in dishes containing water, and the leaves were left to transpire 24 hours at 20 to 25° C. in the shade. The hairy leaf lost 0.646^{gm} of water and the hairless one 0.915^{gm}, which was therefore in the ratio of 1:1.42. The leaves were then exposed to intermittent sunshine for one hour; the hairy leaf now lost 0.08^{gm} and the hairless one 0.167^{gm}, or in the ratio 1:2.09. He concludes therefore that the hairy covering is especially important in restricting the transpiration in sunlight, but that it also operates in a less degree in diffuse light. In the sunshine it probably prevents the extreme heating of the leaf, in diffuse light it retards the diffusion of the air. The error that might be expected from the exposure of uncutinized surfaces, when the hairs are cross-sectioned, HABERLANDT found by mathematical calculation to be insignificant.

BAUMERT[7] tested the heat screening power of hairy coverings and found that in one case a leaf deprived of hair became 37.5 per cent warmer than a normal one.

It was soon found that to obtain experimental data regarding the effectiveness of various coverings was not easy. In fact, it seems almost impossible to obtain accurate and detailed results because of the many factors that enter. No two leaves are exactly alike in size, or in thickness of cutin, or in water content; and it is very difficult to remove the hairy covering for comparative experiments without injuring the tissue of the leaf. Moreover, the stomates may be open at times and closed at others, and the two leaves used may not be alike in this respect.

Fortunately there seemed to be a method of approaching the problem in an indirect way. It is quite generally recognized that by far

6 HABERLANDT, G., Physiologische Pflanzenanatomie. 3. Aufl. 116. 1904, and possibly in earlier editions.

7 BAUMERT, K., Experimentelle Untersuchungen über Lichtschutzeinrichtungen an grünen Blättern. Beitr. Biol. Pflanz. 9:83–162. 1907; and Inaug. Diss. Erlangen. 1907.

the most important factor in transpiration is evaporation; indeed we may say that transpiration is really evaporation modified and regulated by the plant. Therefore, it seemed that a detailed study of the relation of cutin and hairy coverings to evaporation would throw much light on the relation of these same coverings to transpiration.

The first desideratum for such experimental work was a suitable evaporating surface. Several substances were tried, but the choice finally fell on good quality blotting paper. This possessed the desired property of wetting quickly and evenly, and of having a very homogeneous evaporating surface. The pieces used were all cut, for convenience, exactly 7^{cm} square. The plan followed was to expose saturated squares of this paper to the air, each having been previously weighed and then covered with the material to be experimented with. After a given time each was again weighed, and the difference in weight of course represented the quantity of water lost by evaporation. One set of readings in each case was taken in very quiet stagnant air, and another set in air actively in motion. The former condition was obtained by completely inclosing a portion of table top with botanical drying felts placed on edge and covered with the same. For the wind, a small electric fan was stationed at one end of a table on which the evaporating blotters were placed. After a large number of erratic readings were obtained, it was recognized that the following precautions must be taken to eliminate errors. The blotters should be rolled with a round pencil to remove surface water. They should be placed on slightly larger squares of glass and gently rolled again, while with the finger the edges are carefully pressed in contact with the glass. The glass plate and coverings should be weighed with the blotter both before and after. The substance in contact with the blotter should have been previously rendered waterproof in a dilute solution of paraffin in gasoline, otherwise water will be absorbed. The cotton coverings used were always separated from the blotter by a very thin linen cloth so treated. Various materials, in most cases composed of cotton, were used to simulate a hairy covering, but in place of cutin beeswax alone was finally employed. This, while melted, was evenly and thinly spread over the damp blotter with a brush. In order to avoid reducing the supply of water in one case far below that in the other, and thus possibly introducing error,

it was found desirable to conduct the experiments in the wind for only a fraction of the time that they were conducted in still air; but afterward, for comparison, all readings were computed on the basis of quantity lost per hour, and finally on the basis of 1^{gm} lost by the naked blotter per hour. When all the above requirements had been discovered and complied with, a great many readings were obtained in each series, all agreeing within the limits of experimental fluctuation. All the experiments were conducted in the laboratory in February, March, and early April, and therefore in an artificially heated very dry room. The fan was run very rapidly in all cases.

In the following tables the first and fourth columns represent the average quantity in grams lost by each blotter per hour in all the later readings taken. The second and fifth columns show the same quantities reduced to the basis of 1^{gm} for the naked blotter. The retarding effect in the third and sixth columns was obtained by subtracting the loss under cloth, hair, cotton, or wax from the quantity (1^{gm}) lost by the naked blotter. By "increase in efficiency" in the seventh column is meant the number of times greater the retarded effect in wind was compared with the same in still air. The last column represents the number of times this increase in efficiency in wind was greater than the increase in efficiency of wax.

SERIES I.—Coverings used: (*a*) one layer of very thin linen cloth, (*b*) two layers of the same cloth, (*c*) wax coating.

	Still air			Wind				
	Gm per hour	Ratio to 1 gm naked	Retarding, gm	Gm per hour	Ratio to 1 gm naked	Retarding, gm	Increase eff.	Times wax
Naked blotter...	0.398	1.000	.....	4.210	1.000	.....	.....	.....
1 layer cloth....	0.358	0.899	0.101	2.670	0.634	0.365	3.6	2.4
2 layers cloth...	0.338	0.849	0.151	2.110	0.501	0.497	3.3+	2.2
Wax...........	0.181	0.455	0.545	0.780	0.185	0.815	1.5	...

SERIES II.—Coverings: (*a*) one layer thin linen cloth covered with very thin layer of cotton, texture of linen easily seen through the cotton, (*b*) one layer of linen and one layer of thick cotton batting about 2^{cm} thick, (*c*) wax.

Naked blotter...	0.303	1.000	.....	3.310	1.000	.....	....	...
Thin cotton....	0.262	0.864	0.136	1.430	0.432	0.568	4.17	2.7
Thick cotton....	0.219	0.722	0.278	0.870	0.263	0.737	2.65	1.7
Wax...........	0.153	0.505	0.495	0.740	0.223	0.777	1.55	...

SERIES IIA.—Same coverings as in the last; experiment conducted in sunlight, on a black table top.

Naked blotter...	3.700	1.000	.....	6.820	1.000	.....	....	...
Thin cotton.....	2.590	0.700	0.300	3.320	0.486	0.514	1.71	1.4
Thick cotton....	1.410	0.381	0.619	2.110	0.309	0.691	1.11	0.9
Wax...........	1.220	0.329	0.671	1.350	0.198	0.802	1.19	...

SERIES III.—Coverings: (*a*) one layer of outing flannel (cotton), (*b*) one layer thin ordinary flannel, (*c*) wax.

Naked blotter...	0.343	1.000	.....	3.870	1.000	.....	....	...
Outing flannel ..	0.301	0.877	0.123	1.540	0.398	0.602	4.88	3.37
Ordinary flannel	0.300	0.874	0.126	1.880	0.486	0.514	4.08	2.80
Wax...........	0.157	0.457	0.543	0.810	0.209	0.791	1.45	....

SERIES IV.—Coverings: (*a*) one layer mosquito netting, (*b*) wax.

Naked blotter...	0.340	1.000	.....	3.44	1.000	.....	.....	....
Mosquito netting	0.337	0.991	0.009	2.85	0.828	0.172	19.11	12.7
Wax...........	0.160	0.470	0.530	0.69	0.200	0.800	1.51	....

SERIES V.—Coverings: (*a*) human hair soaked in gasoline and paraffin, cut up into 1–3^{mm} lengths, and sprinkled sparingly over a blotter, to simulate a strigose covering, (*b*) wax.

Naked blotter...	0.3444	1.000	.....	3.58	1.000	.....	....	...
Strigose hair	0.3399	0.987	0.013	3.38	0.944	0.056	4.30	2.9
Wax...........	0.1580	0.459	0.541	0.73	0.204	0.796	1.47	...

From the above five series of readings the following may be deduced:

1. Evaporation from an uncovered surface was about 10.6 or 10.8 times as great in the wind of the fan as in still air (series I and II, columns 1 and 4).

2. In sunshine, under the conditions of the experiment, it was only 1.8 times as great in wind as in still air (series IIA, columns 1 and 4).

3. In still air it was 9.3 to 12.2 times as great in the sunshine as in the shade (series I, II, and IIA, column 1).

4. In the wind it was only 1.6 to 2 times as great in sunshine as in shade (series I, II, and IIA, column 4).

5. Hairy coverings of all kinds and thicknesses used were less efficient in retarding evaporation than the layer of wax employed (columns 3 and 6 in all series).

6. All coverings became more efficient in the wind (column 7 in all series).

7. The efficiency of hairy coverings, in thicknesses at all approaching those actually found on leaves, was very slight in still air (series I, II, and III, column 3, line 2, etc.).

8. Such coverings became very efficient in wind (same series, columns 6 and 7).

9. Their efficiency increased in wind much more rapidly than did that of wax (same series, column 8).

10. Even the layer of cotton 2^{cm} thick did not equal the layer of wax as a protective device. In still air the difference between the two was marked, but in wind became less evident.

11. The thinner coverings showed a greater increase in efficiency over wax than did the thicker (cf. column 8 in series I, II, III, IV, and V).

12. Such thin coverings as strigose hairs and mosquito netting produced scarcely any effect in still air, but showed a marked efficiency in the wind, the increase being 4–20 times, which was 2.9–12.8 times that of wax respectively (series IV and V, columns 7 and 8). Both of these materials may retard in wind as much as 5.6 to 17.4 per cent (series IV and V, column 6).

13. The effect of sunshine was marked. In still air the thin and thick hairy covering became 1.5–1.6 times more efficient when compared with wax. In the wind in sunshine the increase in efficiency was not the sum of the increase due to wind in shade and to sunlight in still air, as one might at first expect, but represented an increase in efficiency over still air in shade that was even somewhat less than the increase in wind shade over still air shade (series II, column 3, series IIA, column 6, and series II, column 7).

14. If hairy coverings on leaves behave in the same way as our artificial hairy coverings, we may say that they produce comparatively little effect in retarding transpiration in still air, but have a marked protective action in wind. Thin strigose coverings produce no appreciable effect in still air, but become important factors in wind. A waxy (i.e., cutinized) covering is more efficient, and has a more constant retarding effect at all times. In sunshine hairy coverings are increasingly protective, their increase in efficiency being

also greater than that of cutin in this respect. Their relative efficiency in wind is not markedly different, whether the sun shines or not (series II and IIA, column 6), being somewhat less perhaps in the former case. Their actual protection, of course, is greater the larger the quantity of water lost, i.e., in wind and in sunlight.

Some experiments were conducted with shellac in the place of the waxy coating on the blotter. The shellac was considered to represent more nearly the resinous coatings so frequently spread over leaves and twigs in dry regions. The readings showed the behavior of waxy and resinous coatings to be very similar.

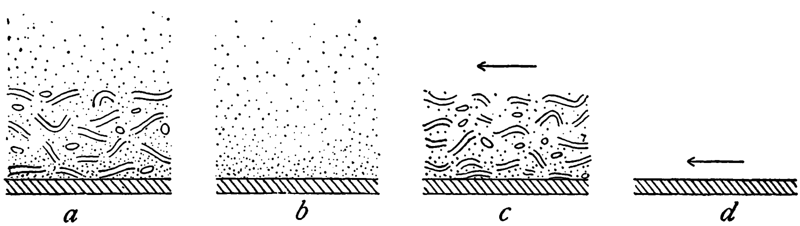

FIG. 1.—Diagrams illustrating the relation of evaporation from naked and hair-covered surfaces in wind and in still air: *a*, hair-covered in still air; *b*, naked in still air; *c*, hair-covered in wind; *d*, naked in wind.

Many readings were taken with actual leaves substituted for the blotters, but in the main they were very erratic. It was found, however, that leaves of Hydrangea and of Nicotiana especially, when covered with layers of cloth and cotton, behaved essentially the same as did the blotting papers. Probably all would have done so if the other factors could have been eliminated.

The reason for the slight efficiency of hairy coverings in still air and their greatly increased efficiency in wind is not at first apparent. The following is the only plausible theory occurring to me. As indicated in the accompanying diagrammatic drawings, in still air a layer of nearly saturated air is soon formed and maintained above the naked as well as above the hair-covered blotter (*fig. 1*, *a* and *b*). If the hair is thin, it is imbedded in this layer, and the latter is modified little if at all by the hair. Evaporation, therefore, with or without the hair, is into an atmosphere of about equal saturation, and therefore should be about the same. If the hair is very thick, then the

saturated layer of air will be somewhat increased and evaporation will be correspondingly retarded.

In wind, however, molecules are immediately blown away from the naked or wax-covered surface (*d*), while in the hairy covering (*c*) there is retained a partially saturated atmosphere. Air currents do not easily penetrate the interstices between the hairs, and the vapor molecules probably find more difficulty in rapidly passing through the hairs. Since evaporation from a surface is in proportion to the saturation of the adjacent atmosphere, it follows that evaporation in diagrams *a* and *b* will differ but slightly, while between *c* and *d* there will be a much greater difference.

Evaporation is also proportional to temperature. It is reasonable, therefore, to expect an increase when the blotter is exposed to the heat of the sun's rays. Hairy coverings act as a screen to the heat rays, and therefore the cooler blotters beneath them evaporate less. It is probable, however, that the effect of sunshine in nature is rarely if ever as great as in our experiments, except possibly in the case of leaves lying flat on the ground, because of the absorbing effect of the black background of the laboratory tables used.

Significance of the results

We are now able to answer at once the first two questions propounded in the introduction to this paper. A protective action of 35–40 per cent in wind with coverings of the thickness of outing flannel certainly warrants us in saying that hairy coverings are sufficiently efficient in retarding loss of water to justify their maintenance on the basis of natural selection. A protection of 5.6 per cent in wind shows also that strigose coverings may materially affect the loss of water. In the case of strigose plants the hairs are usually developed very early, and therefore while the leaves and shoots are small. The hairy covering is therefore more concentrated and denser at this time, but becomes more scattered as the surface increases. As Coville[8] has suggested, such strigose hairs probably function mainly while the organs are young. Hairs which on the mature leaves are scattered far apart may have been of considerable service

[8] Coville, F. V., Botany of the Death Valley Expedition. Contr. U.S. Nat. Herb. **4**:53. 1893.

to the young leaf. It now remains to determine what relation the experiments bear to the solution of the last two questions.

From a consideration of the thin unprotected epidermis of hygrophytic plants, guttation through water pores, root pressure, and possibly other methods of increasing the transpiration stream, we may reasonably infer that most if not all plants find it advantageous to maintain as great a transpiration stream at all times as is consistent with their water supply. From this point of view, plants living in a highly desiccating atmosphere may be divided into two groups. In one group the water supply is very limited; in the other, through the presence of water in the soil, the supply is much greater. It would seem highly advantageous, therefore, for plants of the latter group to possess some mechanism by which the transpiration could be retarded when tending to be so excessive as to exceed the water supply, as for instance in strong dry winds or bright sunshine; but which would allow almost uninterrupted transpiration when the transpiration tends to be less, as at night. Plants of the former group would find continued protection desirable. This they would find in the waxy and resinous coatings, while those of the second group would find hairy coverings better adapted to their needs. If our interpretation is correct, we should expect desert plants with very scanty water supply to be highly cutinized, instead of hairy, while the hairy desert plants would be found in some way connected with a greater supply of subterranean water. Such a hairy plant in the desert might be supposed to act as follows. During the day the hot dry winds blow and the sun shining upon the leaflets tends still further to increase the transpiration. The requisite protection is now afforded by the hairy covering; but at night the winds die down, the atmosphere becomes humid, dew falls, and transpiration becomes more difficult. At such times the hairy covering does not materially impede the transpiration.

Known facts do not seem opposed to this interpretation, but rather in its favor. The writer has had no opportunity to determine the available water supply of desert plants, but an inspection of COVILLE's Death Valley report shows that the habitat of a great majority of the characteristically hairy shrubs cited (p. 52) is given as either dry river bottoms, lake shores, or high on the mountains.

Two densely canescent plants are cited particularly as occurring near timber line on Mt. Whitney (p. 55). Since the mountains according to this report (pp. 22 and 42) are not so arid as are the lowlands, and the soil is generally more moist, all three habitats, therefore, are likely to possess considerable soil moisture. However, to draw generalizations from a report is unsatisfactory, since so much depends on depth of root system, persistence of foliage, etc. Special study of individual conditions in the Death Valley is really necessary.

In the eastern United States, where conditions are mesophytic, hairy plants are found mainly on dry exposed gravelly or sandy knolls and hills, as for example *Verbascum Thapsus*, various species of Antennaria, Gnaphalium, Anaphalis, *Solidago bicolor*, and *S. nemoralis*. Here drying winds and hot sunshine prevail during the day, but at night the air is still and damp. The soil is not excessively dry, but the Verbascum, to still further guard against danger, possesses a long tap root which descends to a considerable depth, where a sufficient supply of water is assured. A hairy covering, therefore, would best meet the needs of such plants.

The most complete account of the occurrence and function of hairy coverings seems to be that given by KERNER.[9] He seems to have believed that the hairy covering so frequently on the under side of the leaf alone could be of functional importance only when bathed with sunlight. To explain this difficulty he showed how when the dry winds blow violently the leaves of the side facing the wind all become inverted, so that the silvery under surface faces the sun. The present experiments show, on the other hand, that the protective action of the hair covering the stomate-bearing surface would be great in wind without sunshine. The inversion of the leaves is not necessary to explain the functioning; indeed, it is doubtful if such inversion continues long enough to be of any great importance. The more important fact is that the hairs cover the stomate-bearing surface rather than the upper surface.

KERNER says that hairy coverings are especially pronounced in the Alps and in the Mediterranean region, but are almost absent from the arctic region. He says that the relation between hairy coverings and transpiration stands out strikingly in those districts

9 KERNER, A., AND OLIVER, F. W., The natural history of plants 1:313.

where plants during their vegetative period are as a rule exposed to dry air for only a few hours each day, and where their activity is not interrupted by a warm dry period but by frost and cold. On the Alps the complete drying-up of plants by the sun is rare, but the dry winds and hot sun at times make a lessening of the transpiration very desirable. On other mountains of the same latitude in Europe and Asia many hairy plants occur. Indeed, the account given by KERNER is almost an exact picture of what we should expect from the point of view of the present experiments. On the slopes and in the pockets on the Alps, where vegetation exists, the soil is warmed in summer and there is probably an available supply of water throughout the vegetative period.

Quite different is the condition in the arctic regions. Thick evergreen leaves replace the hairy ones. KERNER says: "When hairy coverings are present they are restricted to the under surface, especially to that of rolled leaves. They are never found on plants of rocky slopes, but only on those of damp marshy ground, or by the side of water which is for a short time free from ice." He believes that such coverings are not concerned with transpiration at all, and that the absence of hairy coverings in the arctic regions is due to the moisture in the soil and the consequent absence of danger of drying out. This explanation, however, seems insufficient. If it were true, why should we find thick, highly cutinized, xerophytic leaves on such plants as Diapensia, Empetrum, Vaccinium, etc.? Our explanation now would be that the soil in the arctic regions is too cold for root absorption even in summer, since it remains frozen only a few inches below the surface. The water even if present is therefore not readily available, and there is constant physiological dryness. These are exactly the conditions necessary to demand a cutinized rather than a hairy flora.

Our evergreen leaves, such as those of Rhododendron and Kalmia, are heavily cutinized, not tomentose. According to our theory this would be owing to limited water supply in winter, which is true. Owing to the coldness of the soil and the inactivity of all the living cells of the plant, there is constant physiological dryness.

Plants of the great plains, where the wind is excessive but the ground not extremely dry, are commonly silky, strigose, or tomentose.

Plants of the eastern peat bogs find difficulty in absorbing water, possibly because of toxic substances in the soil, and these are cutinized, not hairy (except Ledum).

KERNER emphasizes the prominence of hairy plants in the Mediterranean region and notes that they are not so numerous in the adjacent steppe region, because "in the steppes and deserts the dryness of the summer is greater, and even thick hairy coverings are not always a sufficient protection against this dryness; and also because in some districts the dry period passes directly into a severe winter." In the Mediterranean region, as the dry summer follows the rains of winter and spring, "their transpiration is very active in consequence of the rapidly increasing temperature of the air, but the saturated soil provides a sufficient substitute for the evaporated water." Toward midsummer, as the drought increases, "if such a plant is to be protected from drying up, its transpiration must be lessened. This is effected by various protective arrangements, but best of all by a thick coating of hair." Very interesting are the biennial plants cited by KERNER. The leaves of these plants formed the first year must pass through the summer and so are abundantly hairy, while those of the leafy flowering shoot the second spring are green instead, because this shoot dies before the summer begins. The whole of KERNER'S account of Mediterranean plants is just what we should expect from the standpoint of the present experiments. There is sufficient water in the soil at all times to make moderate transpiration possible even in summer. At times when this supply is at its minimum and when the sun and wind are exceptionally drying, the leaves are protected from too excessive transpiration by the hairy covering.

GOEBEL,[10] in describing the flora on the Venezuelan Andes between tree line and snow line, remarks on the great number of hairy plants. The white-woolly rosettes of certain species are characteristic of the landscape. The climate here is subject to great and frequent changes from rain, snow, or fog, to sunshine and an exceedingly drying wind. The temperature varies also from 0° to 18°. The soil contains plenty of water, with frequent puddles standing on the surface. The soil is cold and absorption is slow, but the transpiration at times

[10] GOEBEL, K., Die Vegetation der venezolanischen Paramos. Pflanzenbiolog. Schilderungen **2**:1. 1893.

is great. This is a fine picture of just such conditions as we should expect would demand hairy plants; absorption somewhat below normal, transpiration at times excessive, and at other times, as in foggy weather, very slight.

The use by epiphytic plants of cutin rather than hair for retarding transpiration is well known. Even though the air is humid, the scantiness and uncertainty of the water supply actually obtainable by the plant warrants the employment of cutin. The most notable exception is the Florida moss (*Tillandsia usneoides*), the ecological relations of which I have not been able yet to fully make out. It seems probable, however, that the excessive development of the scaly absorbing glands of the leaves is for still further increasing the efficiency of absorption, rather than primarily to retard transpiration.

Hairs are provided on growing shoots and unfolding leaves to retard the transpiration during windy and sunny times in spring, before the cutin has become fully developed. Some plants make use of resin for this purpose instead (e.g., Larrea in the desert, and Gaylussacia in New England). It is probable that in these cases a more efficient covering is here desired. Such resinous coverings may be superior to cutin in that they may be easily shed or be much interrupted when their early protective action is no longer desired. This actually takes place in both of the above-named examples.

In regard to the last question propounded in the introduction, whether the relation to light or to loss of water has been the principal factor in the evolution of hairy coverings, the following facts may be cited. In practically all cases where one leaf surface is devoid of hairy covering it is the upper. Such cases are very common, e.g., Ledum, Antennaria, Quercus, etc. This would not be true if the primary function was as a light screen. Instead, the covering is maintained over the stomate-bearing surface. The multitude of such cases makes it seem almost obvious that the main function of hairy coverings lies in their relation to transpiration, not to the intensity of the light.

From the foregoing statements it is not to be understood that wherever conditions are as described only hairy plants are to be expected, and that in a given locality plants should be either all

hairy or all cutinized, or even that hairy and smooth individuals of the same species should not be found occasionally side by side. If we go more into the details of distribution than into the consideration of the general trends of vegetation and the general examples already given, we must then consider the individual plants; for it often happens that species growing side by side may in one case have a deep root system reaching ground water, in the other have a root system confined to the driest superficial layers of the soil. It is also conceivable that there may be inherent physiological differences between species, and even between individuals of the same species, calling for variations in the amount and kind of protection. The life economy must be studied out in each individual case. We must not fail to remember, also, that the whole seasonal cycle, as well as the life cycle of the individual, must be considered before a full conclusion may be drawn; for a hairy covering which seems not to fit into the general scheme may have done so at an earlier period of development or in an earlier season.

General conclusions

The evaporation experiments outlined in this paper tend to show that porous coverings like cotton, wool, or hair must be very thick to produce any appreciable effect in retarding evaporation if the surrounding atmosphere is quiet, but become very efficient even in thin layers when the air is in motion. On the other hand, a waxy covering is effective at all times, though of course somewhat more so in wind. In sunshine, also, the hairy covering shows a greater increase in efficiency than does wax.

It seems probable that those plants employ a hairy covering to retard transpiration that live in situations where a moderate water supply is available, but where transpiration must be reduced in excessively dry times, but not interfered with when the surrounding air is damp and transpiration therefore difficult. Cutin, on the other hand, is probably employed when there is considerable danger of too great desiccation at all times.

A contemplation of the general occurrence of excessively hairy plants lends probability to this view.

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